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BULLETIN
OF THE
TORREY BOTANICAL CLUB

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The embryology of *Rhizophora Mangle*

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(WITH PLATES 22 AND 23)

The peculiar habit of the mangrove (*Rhizophora Mangle* L.), of germinating the seed while yet on the tree, has attracted considerable attention, and it has been the subject for observation and investigation by a number of persons. The most important investigations on the embryology were made by Karsten * on this and related species and genera, and on species which have similar habit but are classed in entirely different families ; but the results of his work on this particular species were very meager.

The study of this species presents many difficulties, and it was only after repeated efforts that the author succeeded in getting the preparations on which this paper is based. A few stages are missing, but since it is impossible for the author to secure more material at this time it was thought best to publish the results of the investigations.

In general it may be said that the picric acid killing and fixing agents were most successful, but the preparation which gave the best results was a mixture of 98 c.c. saturated aqueous solution of picric acid with 2 c.c. sulphuric acid.

Only one of the four ovules is fertilized (FIGURE 1), and this grows while the other three atrophy (FIGURE 13). The ovaries and ovules did not always increase in size with the same rapidity, so that it was not always possible to judge the age and condition of the internal structures by the size of the ovary or ovule, as will

* KARSTEN, G. Ueber die Mangrove-Vegetation im Malayischen Archipel. Eine morphologisch-biologische Studie. Bibliotheca Botanica, Heft 22 (5 : 1-71). 1891.
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be seen by a comparison of FIGURES 4 and 5, in which the smaller is the more advanced, or by comparison of FIGURES 21 and 22, in which the two structures are of about the same age. It was impossible to determine positively the origin of the archesporium, but it was apparently sub-epidermal (FIGURE 18). One or two tapetal cells are cut off, but whether they ever exceed this number or not the author is unable to say. Karsten figures two each in *R. mucronata* and *Bruguiera eriopetala* and one each in *B. caryophylloides* and *Ceriops Candolleana*. At this time the two integuments were just appearing (FIGURE 2). The archesporial cell enlarges with the enlargement of the nucellus, but the integument undergoes the most rapid growth (FIGURES 3, 19). The ovule continues to increase in size and the archesporial cell divides into megaspores. My only satisfactory preparation of this stage showed three megaspore-cells (FIGURE 20), but it is impossible to say whether this is or is not the regular number. Karsten figures four for both *R. mucronata* and *C. Candolleana*. The nucellus is always small as compared with the size of the ovule. My material was unsatisfactory for following the development of the embryo-sac; however, its formation results in the complete destruction of the nucellus (FIGURES 5, 21). Karsten figures the same condition in this species and in *Carallia integerrima*. In the eight-nucleate stage it was impossible to do more than work the details of the egg-apparatus (FIGURES 21, 22), which were in every way like the normal egg-apparatus. The author did not succeed in finding the polar nuclei or antipodal cells, but found what was apparently the primary endosperm-nucleus (FIGURE 23) lying in the micropylar end of the sac. It was impossible to follow the early divisions of the endosperm, but from this point the preparations were quite satisfactory.

EMBRYO AND ENDOSPERM

The growth of the ovule and ovary is now quite rapid. The embryo-sac increases in size both as a result of growth of the ovule and by destruction of the inner integument, so that we now have a sac enclosed only by the outer integument, filled with an enormous amount of endosperm, in the micropylar end of which is a small embryo (FIGURE 6). At this stage the other

three ovules are in an advanced stage of degeneracy (FIGURE 7). The cells of the endosperm appear to radiate rather indefinitely from a central point in the sac (FIGURE 6). The growth of the embryo may be divided into three periods: (1) first growth of the cotyledons, (2) growth of the hypocotyl, (3) second growth of the cotyledons. The youngest embryo secured was pear-shaped with well-developed suspensor, but was not attached to the wall of the sac (FIGURES 6, 8). The suspensor persists until late in the development of the embryo (FIGURES 8, 9, 14). Apparently the embryo had originated as a series of cells in linear arrangement and developed in accordance with the capsella type. The only embryo of this species figured by Karsten is somewhat younger than this one but does not show a suspensor. The cotyledonary end of the embryo grows quite rapidly and is sometimes quite regular in outline (FIGURES 9, 11, 12) but more frequently is very irregular (FIGURE 10) and apparently very much crowded by the surrounding structures. At a point in the longitudinal axis of the embryo and not far from the suspensor, the cells are very small and very numerous (FIGURE 9, *x*). In a short time the separation of certain cells at this point gives rise to the plumule (FIGURES 10, 12, 24); this is only discernible in section. The cells on the side next to the root-tip are smaller, contain more protoplasm, and are apparently more active than those on the cotyledonary side (FIGURE 24). The endosperm is very thin but the cells of the integument which come in contact with it are very protoplasmic (FIGURE 25). This union between the endosperm cells and the integument is very close; frequently through shrinkage of the internal structures there would be a separation of cells, but this was usually within the integument and not between the cells of the endosperm and the wall of the sac (FIGURE 25). The growth of the cotyledonary part of the embryo results in the pushing of the opposite end of the embryo and part of the endosperm out through the micropyle, and they now lie within the cavity of the ovary (FIGURE 12). The endosperm over the surface of the cotyledons is now very thin, thus bringing them into close contact with the walls of the sac (integument) (FIGURE 12). The cells of that part of the endosperm which has been forced from the sac show a rather indefinite arrangement in rows extend-

ing obliquely from the surface of the embryo outward and upward towards the integument (sac), indicating that the growth of the embryo has exerted great pressure on them (FIGURE 12). Up to this time there has been very little modification in the surface cells of the cotyledons; they are more protoplasmic than the inner cells but otherwise not materially different (FIGURE 26). The growth of the cotyledons now almost entirely ceases and the second period of growth, or growth of the hypocotyl, begins. The hypocotyl grows very rapidly, pierces the apex of the ovary and forms the long pendulous structure, which is frequently eight or ten inches in length (FIGURES 14, 17). The plumule (FIGURE 15) and the vascular tissues of the cotyledonary structure which originated considerably earlier (FIGURE 10, *v.s.*) become more prominent and important. The entire cotyledonary structure undergoes considerable change; the cells appear to contain more protoplasm and stain more deeply. The surface cells and those near the surface become very much elongated with their long axis at right angles to the surface (FIGURE 27). All these modifications are probably for the increased activity of these cotyledonary structures, which undoubtedly absorb great quantities of food for the development of the long hypocotyl. At about this same time numerous masses or strands of very much elongated cells are formed, which lead from the surface cells to the vascular system of the cotyledons (FIGURE 16). A more careful examination of these strands of cells shows them to be of the same character as the vascular system (FIGURES 29, 30), and the author suspected that this system contained more or less sieve tissue but was unable to decide positively on that point. Just before the separation of the hypocotyl from the cotyledonary structure, traces of tracheary tissue (FIGURES 29, 30) appear but it is never very abundant. The endosperm over the surface of the cotyledonary structure becomes very thin with the corresponding slow growth of these organs during this period, and the cells of the integument (wall of sac) are very rich in protoplasm (FIGURE 28).

When the hypocotyl is about three inches in length, about two-thirds of the cotyledons are imbedded in the embryo-sac, and the remaining part in the ovary-chamber, surrounded by a thin layer of endosperm, while the hypocotyl projects through the apex of

the ovary (FIGURE 17). As the embryo approaches maturity, the cotyledonary structure sets up a second growth which pushes the point of union between the cotyledons and the hypocotyl beyond the apex of the ovary. The cotyledons and the hypocotyl then separate and the hypocotyl drops, carrying with it the plumule; while the ovary, containing the outer integument (sac) and cotyledons, remains hanging on the tree.

It is very evident that the cotyledons perform an important function in supplying food to the growing hypocotyl. The disintegration of the nucellus and inner integument and the formation of the enormous endosperm are all important in the nourishment of the embryo during the early part of its development. This may be readily traced by comparing FIGURES 2, 3, 4, 5, 6, 12, and 17; first we have the beginning of the nucellus and both integuments (FIGURE 2) followed by an increase in size of the ovule in which the nucellus is very small (FIGURES 3, 4), then the disintegration of the nucellus to form the embryo-sac (FIGURE 5), the enlargement of the ovule and disintegration of the inner integument (FIGURE 6), a further enlargement in which about one-third of the embryo and a considerable part of the endosperm are forced out of the embryo-sac (inner integument) and lie in the chamber of the ovary (FIGURE 12), and lastly an elongation of the hypocotyl and diminution of the endosperm (FIGURE 17).

SUMMARY

1. Four ovules, but only one fertilized.
2. Archegonium probably subepidermal and cutting off two tapetal cells.
3. Megaspores probably four in number.
4. Completion of embryo-sac results in complete disintegration of the nucellus.
5. Further growth of embryo-sac results in complete disintegration of the inner integument and formation of a large amount of endosperm.
6. Embryo has easily recognized suspensor and is probably of the capsella type.
7. The growth of the embryo may be divided into three periods: (1) first growth of the cotyledons, (2) growth of the hypocotyl, (3) second growth of cotyledons.

8. During first period of growth about one third of the embryo and the greater part of the endosperm are forced out of the embryo-sac and lie in the chamber of the ovary.

9. The second period of growth is confined largely to the hypocotyl, but during this time the structure of the cotyledons undergoes great modification.

10. This modification of the cotyledons is undoubtedly for the purpose of absorption.

11. During the third period of growth, the cotyledons elongate and the point of union between them and the hypocotyl is forced beyond the apex of the ovary.

The greater part of this work was done in Cuba, but it was finished in the laboratory of the New York Botanical Garden. The material was collected at Mariel, Cuba, and herbarium specimens have been deposited in the herbarium of the said garden.

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Explanation of plates 22 and 23

Figures 1 and 17 are purely diagrammatic, made with the aid of a hand lens. Figures 6, 7, and 12-16 are semi-diagrammatic, made with the aid of a very low power lens in a compound microscope. Figures 2-5 and 8-11 were made with Spencer's 4/ ocular and 2 mm. objective. Figures 24-29 were made with Spencer's 8/ ocular and 4 mm. objective. Figures 18-23 and 30 were made with Spencer's 8/ ocular and 16 mm. oil immersion.

Fig. 1. Cross-section of ovary showing four ovules.

Fig. 2. Young ovule showing archesporium and origin of integument. (See Fig. 18.)

Fig. 3. Young ovule showing archesporium and integuments. (See Fig. 19.)

Fig. 4. Young ovule showing megaspore and integuments. (See Fig. 20.)

Fig. 5. Ovule showing disintegration of nucellus in the formation of the embryo-sac; also the integuments. (See Fig. 21.)

Fig. 6. Embryo-sac containing embryo (*e*), endosperm (*end*), somewhat shrunken and enclosed in the outer integument (*o. i.*), the inner integument having undergone disintegration. (See Fig. 8.)

Fig. 7. Atrophied ovule. Same age as figure 6.

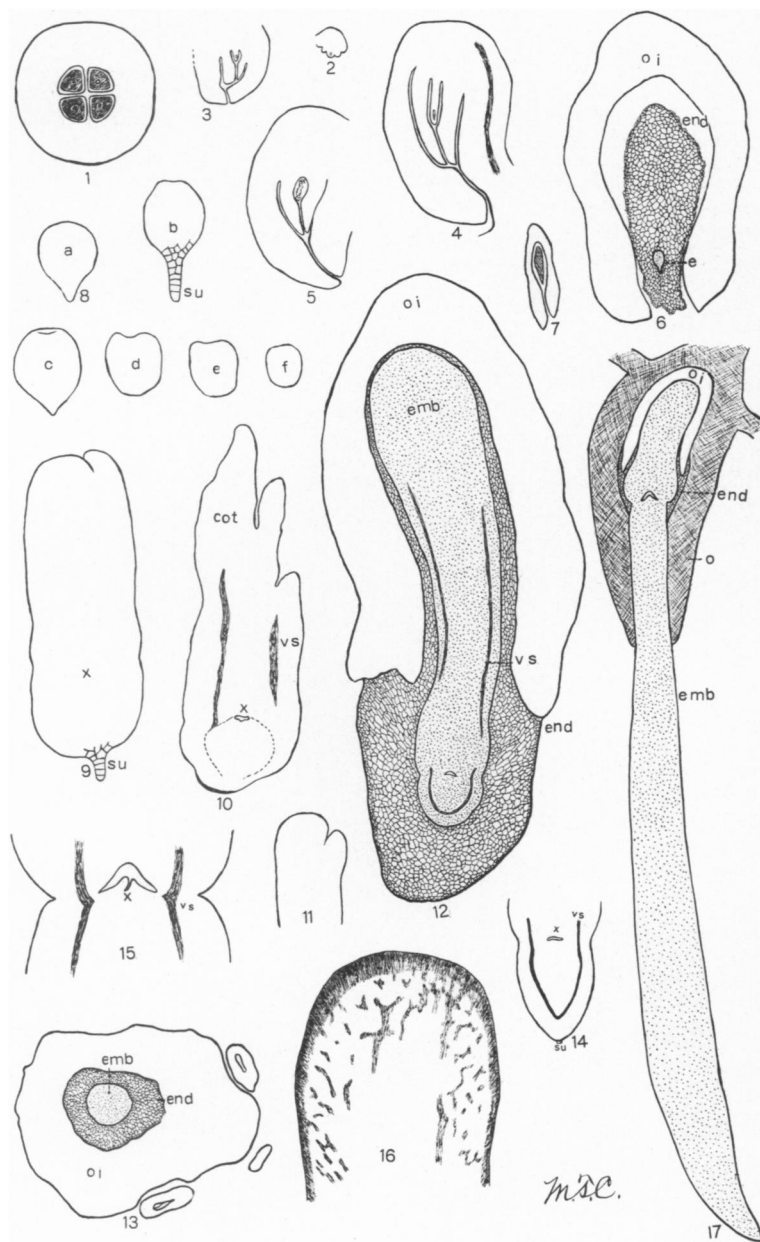
Fig. 8, *a-f*. Embryo in serial sections showing suspensor (*su*). Same preparation as figure 6.

Fig. 9. Embryo showing suspensor (*su*), prominent cotyledonary structures and point of origin of the plumule (*x*).

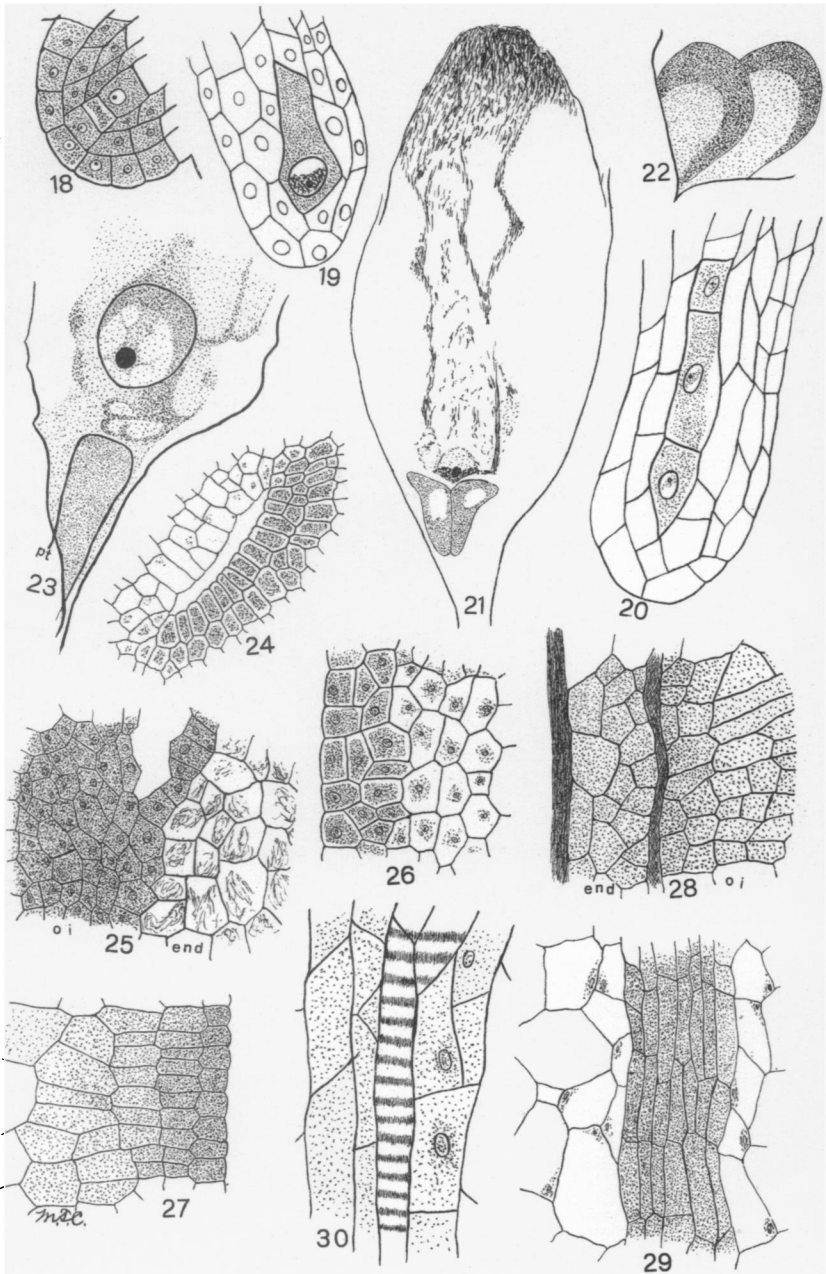
Fig. 10. Embryo showing irregular cotyledonary structures (*cot*), plumule (*x*), and vascular system (*v. s.*).

Fig. 11. Tip of cotyledonary structure. About the same age as figure 10.

Fig. 12. Embryo (*emb*), surrounded by endosperm (*end*), and partially enclosed in the sac which is composed of the outer integument (*o. i.*).



EMBRYOLOGY OF RHIZOPHORA



EMBRYOLOGY OF RHIZOPHORA

Fig. 13. Cross-section of ovary showing the one fertile and the three sterile, degenerating ovules; embryo (*emb*), endosperm (*end*), and sac (*o. i.*). About the same age as figure 9.

Fig. 14. Part of embryo showing plumule (*x*), vascular system (*v. s.*), and suspensor (*su*).

Fig. 15. Part of embryo showing plumule (*x*) and vascular system (*v. s.*).

Fig. 16. Tip of cotyledon showing vascular system and connections with the surface.

Fig. 17. Diagrammatic drawing showing relation of parts; embryo (*emb*), endosperm (*end*), sac or outer integument (*o. i.*), and ovary (*o*).

Fig. 18. Archesporium and two tapetal cells. From same preparation as figure 2.

Fig. 19. Archesporium. From same preparation as figure 3.

Fig. 20. Nucellus and megasporos. From same preparation as figure 4.

Fig. 21. Embryo-sac showing egg-apparatus. From same preparation as figure 5.

Fig. 22. Egg and one synergid.

Fig. 23. Part of embryo-sac showing endosperm-nucleus and pollen-tube (*p. t.*).

Fig. 24. Plumule. From same preparation as figure 10.

Fig. 25. Endosperm (*end*), and part of the wall of the sac or outer integument (*o. i.*). From the same preparation as figures 10 and 24.

Fig. 26. Surface of cotyledon. From same preparation as figure 12.

Fig. 27. Surface of cotyledon showing modified columnar cells. From same preparation as figure 16.

Fig. 28. Endosperm (*end*) and integument or wall of sac (*o. i.*). From same preparation as figure 16.

Fig. 29. Vascular system. Same age as figure 16.

Fig. 30. Vascular system showing formation of tracheary tissue. Same age as figure 29.